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WEATHER AND THE LABILITY OF BREEDING POPULATIONS OF THE CHECKERED WHITE BUTTERFLY, *PIERIS PROTODICE* BOISDUVAL and LeCONTE

ARTHUR M. SHAPIRO

Department of Zoology, University of California, Davis, California 95616

ABSTRACT. In the Sacramento Valley and Sierra Nevada of northern California, *Pieris protodice* populations experience frequent colonizations and extinctions. Overwintering success and colonization rate are roughly correlated with weather. "Permanent" populations exist in local areas of dredge tailings habitat; these are the sources of each year's first colonizers. The Ehrlich and Birch "mosaic" model of population regulation appears to be a good description of the dynamics of *P. protodice* populations.

INTRODUCTION

Two controversial areas of theoretical population biology —island biogeography (MacArthur and Wilson, 1967) and group selection (Wynne-Edwards, 1962; Williams, 1966) — revolve to a substantial extent on the question: "How permanent are natural populations of plants and animals?" A high turnover of local populations is theoretically conducive to rapid evolution and speciation. Defensive adaptations of plants and host-selection patterns in herbivorous insects have been linked to rates of population turnover (Feeny, 1975). For all these reasons data on the permanence or impermanence of populations are highly desirable, but unfortunately scarce in many otherwise well-studied groups of organisms.

The butterflies have received a tremendous amount of attention from population biologists, but population-turnover data are few. Ehrlich *et al.* (1975) summarized 15 years of tracking the Jasper Ridge population of *Euphydryas editha* Boisduval (Nymphalidae). During this time local subpopulations repeatedly

waxed and waned sometimes asynchronously, with at least one extinction. Ehrlich *et al.* (1972) described the impact of anomalous weather on various organisms at Gothic, Gunnison County, Colorado: one of the casualties of an unseasonal snowstorm was a population of *Glaucopsyche lygdamus* Doubleday (Lycaenidae) which was apparently eradicated. The ups and downs of British Lepidoptera are chronicled in the *Entomologist's Record,* and some are summarized by Ford (1957).

Against this evidence for population lability there are isolated colonies of butterflies which have been observed by generations of collectors and whose "stability" is proverbial. In the United States a good example is the Coy Glen population of *Asterocampa clyton* Boisduval and LeConte (Nymphalidae), which has seemingly persisted for over 35 years in central New York near the species boundary (Shapiro, 1974c). Bonafide relict populations on mountaintops, in peat bogs, and on sand barrens obviously demonstrate long-term persistence (thousands of generations) since the probability of recolonization under present ecological and climatic conditions is so low.

The distinction between high- and low-turnover populations may correspond to that between r- and K-selected species (MacArthur and Wilson, 1967; Force, 1974). The relative importance of density-dependent and density-independent controls is thought by many authors to vary between them. Ehrlich and Birch (1967) proposed a "mosaic" model of population regulation which incorporates both types of control. The essential features of this model have been summarized concisely by Ricklefs (1973: p. 475):

> They suggested that populations should be thought of as consisting of a mosiac of numerous (sub) populations that receive occasional immigrants from other areas but are otherwise independent. If a local population became extinct by chance fluctuations in size, it could be re-established by colonization from surrounding populations . . . while extinction may occur by chance, the colonizing ability . . . depends on how many areas of habitat are free of individuals. When the population is sparse, many local areas are available for recolonization; when it is dense, few areas are unoccupied . . . the tendency to increase through colonization of new areas is density-dependent.

This model appears to simulate processes which are thought to occur in many butterfly populations. Its applicability to the dynamics of populations of the Checkered White, *Pieris protodice* Boisduval and LeConte (Pieridae), is described below.

CHARACTERISTICS OF THE CHECKERED WHITE

Pieris protodice is a common butterfly over most of the United States except New England and the Pacific Northwest (Shapiro, 1976). It is usually found in disturbed habitats, including desert washes, ocean beaches, and urban vacant lots. Over most of its range it occurs at low to moderate altitudes; its upslope and northward restrictions imply climatic intolerance. Its host plants are weedy Cruciferae, native and introduced, annual and perennial. Over most of its range it prefers species of *Lepidium* where available. In lowland California its most important host is *Brassica geniculata* (Desf.) Ball. It is multivoltine everywhere in its range, with up to six generations a year in lowland California and two to three in the mid-Sierra Nevada at 1500-2000 m. (Shapiro, unpub.)

The Checkered White has some reputation as a fugitive species; the unpredictability of its occurrence was noted by Clark and Clark (1951), Rawson (1945), and Maeki and Remington (1960). Tilden (1965) says it "may be found most of the year . . . in every back yard and farm lot" in the San Francisco Bay area; but in many years it cannot be found in the Bay area at all. The California literature gives a misleading impression that *P. protodice* is ubiquitous and always common. Actually it has probably been taken throughout the state, but is often absent from entire counties for entire years or parts of years.

Since 1972 sampling has been done on a year-round, weekly to biweekly basis at selected sites in Yolo, Solano, and Sacramento Counties, northern California, at a constant level of effort as part of a long-term community phenology study (Shapiro, 1975a). A by-product of this sampling has been detailed documentation of the spatial and temporal distribution of the 55-odd species in the breeding butterfly fauna of the Valley. The fauna is mostly multivoltine and decidedly weedy (Shapiro, 1974a) and many of the species show dramatic year-to-year population fluctuations, but none so dramatic as that of the Checkered White. Similar patterns occur in *Lerodea eufala* Edwards (Hesperiidae), *Brephidium exilis* Boisduval (Lycaenidae), and *Precis coenia* Hübner (Nymphalidae), as well as others, but their biology is less well known.

THE CHECKERED WHITE IN THE VALLEY

The Checkered White has been taken throughout the entire length of the Sacramento Valley, but it occurs reliably and overwinters predictably only on the dredge tailings along the east side of the Valley. This unnatural habitat dates to early in this century when "large gold dredgers floated in artificial ponds in broad stream valleys and flat lands bordering the western foothills (of the Sierra Nevada) to excavate the gravel below the surface. When the 'washings' emerged from the dredgers (after separating out the gold), the soil particles went to the bottom and huge mounds of large creekworn boulders were piled on the surface of the land . . . Several decades are required for enough air-borne soil to accumulate on the boulder heaps so that plants and trees can take root" (Storer and Usinger, 1971). The resulting landscape has provided a refuge for native plants and animals in a largely urbanized and agriculturalized region. The restriction of *Pieris protodice* as a permanent resident is not, however, due to lack of suitable breeding habitat elsewhere. Its host, *Brassica geniculata*, is very common on the tailings but also occurs widely elsewhere on sandy loam soils. In most years breeding colonies of the butterfly may be found far from the dredge tailings, on *B. geniculata* and other Crucifers, but they do not persist into a second season. As discussed below, most local extinctions appear to occur over winter, suggesting that the diapausing pupa is subject to the "key" mortality factor. Although larvae can be found at almost any time in exceptionally mild winters, normally overwintering occurs only in the pupal state. Its facultative diapause, under the control of larval photoperiod and temperature exposure, is of low intensity: diapausing pupae (induced under 10L:14D with day and night temperatures of 17.5°C and 10°C) removed to 25°C on their seventh day generally eclose in 4-9 weeks. As Tauber and Tauber (1976) have shown, diapause terminates in midwinter in most insect populations. For such a weak diapauser near the northern edge of its range, vulnerability to weather-induced winterkill may be very great.

A CAVEAT

This paper does not pretend to be a rigorous demonstration of causation, or even of statistical correlation, between weather and

population levels. It is, rather, a qualitative presentation of a *plausible* pattern of causation for the observed facts, i.e., the presence or absence of the Checkered White at the study sites throughout the years 1972 through 1977, and the much-publicized drastic fluctuations in northern California weather during that period, which includes the 1975-77 drought. Of the populations discussed here, precise estimates of density, based on mark-release-recapture studies, are available only for two, and not in all years. The narrative which follows presents trends in abundance based on eyeball estimates — essentially and inescapably subjective, but made as validly comparable as possible by an experienced observer following consistent procedures. Because all butterfly species present were being monitored phenologically at each site, the effort involved in tracking population levels at the level of rigor applied to Ehrlich's univoltine, circumscribed *Euphydryas* was out of the question.

Identification of the relevant weather elements is also difficult. When numerical population estimates are available, multiple regression and correlation techniques can be applied to identify those weather elements most useful in prediction. First-flight data do not lend themselves to such treatment unless very long runs of data are available. Commonly in ecological studies, weather data from the nearest recording station of the government meteorological service, or from a limited-scope station set up at or near the study site in a conventional instrument shelter by the investigator, are reported and create an illusion of rigor. The most meaningful data for studies of overwinter survival of butterfly pupae or reproductive success of adults involve sophisticated measurements of aspects of ground-level and boundary-layer microclimatology. Table 1, containing an abstract of climatological data for one location within the study area (Executive Airport, Sacramento, NWS recording station), gives the sort of data actually available. Although trends are obvious to residents, and to climatologists having access to data from many stations, idiosyncratic aspects of local data not uncommonly obscure them when one or a few stations are used. Data of this sort are thus simultaneously too coarse-grained (relative to microclimate) and too fine-grained (relative to local departures from regional patterns) for confident use. The Sacramento data are provided to convey a general picture of weather in the study area, but because they are inherently inadequate to do so a nar-

rative summary for the three-county area is coupled with the butterfly observations. West Coast rainfall-pressure patterns throughout the period are discussed regularly in the *Monthly Weather Review.*

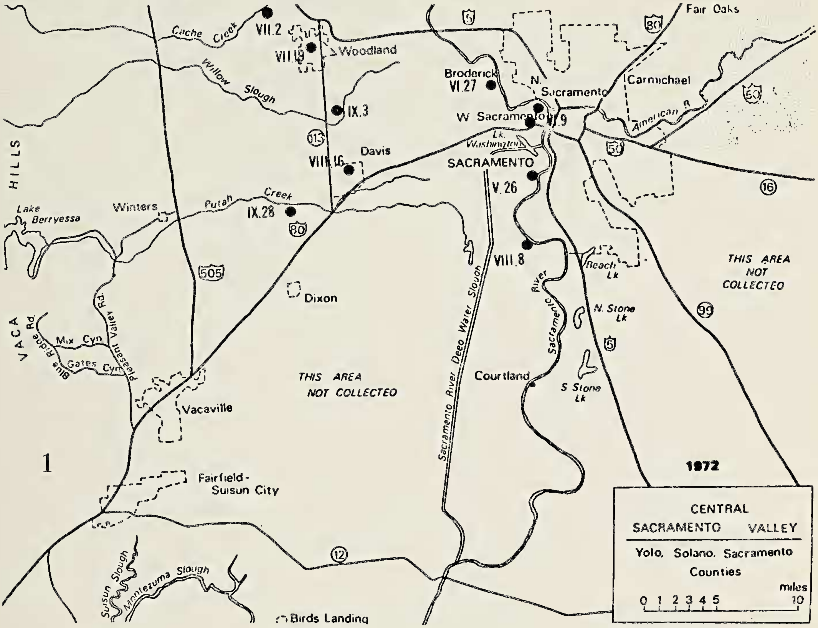
Neither monthly temperature or rainfall data, nor their deviations from the arbitrarily selected 30-year means, directly affect butterfly survival except in rare extreme cases. Outright thermal lethality is almost never observed. The day-to-day distribution of temperature, rainfall, dew, cloudiness and wind determines survival and reproductive success and growth rate, operating at and near ground level, and these aspects of "butterfly weather" are very difficult to extract from climatological data summaries. Although no specific data are available for *Pieris,* pupal death due to bacterial and fungal parasites is believed to increase dramatically under mild (7°C) and wet winter conditions. A variety of *sequences* of individually innocuous events can be lethal to post-diapause pharate adults (uneclosed adults within the pupal case, ed.), just as rain or frost on two or three critical days can prevent effective pollination of a fruit-tree crop — a critical event not readily apparent from columns of means and deviations. With adequate numerical population estimates and microclimatic data whose collection has been imaginatively designed in advance, more rigorous assessments of the role of different weather elements in insect population dynamics are thoroughly feasible. The overall pattern of how, say Checkered White populations behave — as presented here — is *not,* however, inferable from the dynamics of any single, local population, no matter how well quantitated.

HISTORY IN THE VALLEY, 1972-77

Figures 1 - 6 show the first dates when *Pieris protodice* was recorded at sites away from the dredge tailings from 1972-1977. It is immediately clear that there is great year-to-year fluctuation in first-flight dates. Since *P. protodice* is obligately multivoltine, it would appear that (from the frequency of absences) a high turnover rate of local populations must exist.

The autumn of 1971 was prolonged, warm, clear, and dry; the winter, mild and dry. *Pieris protodice* first appeared in western Sacramento and adjacent Yolo County in late May - early June 1972, with no evidence of overwintering in these locations. The summer was hot and dry. Despite an early start and gener-

Figures 1 - 6. First dates of capture of *P. protodice* at sampling stations in the Sacramento Valley from 1972 through 1977. Dredge tailings (Rancho Cordova) are stippled. 1 mile = 1.61 km.



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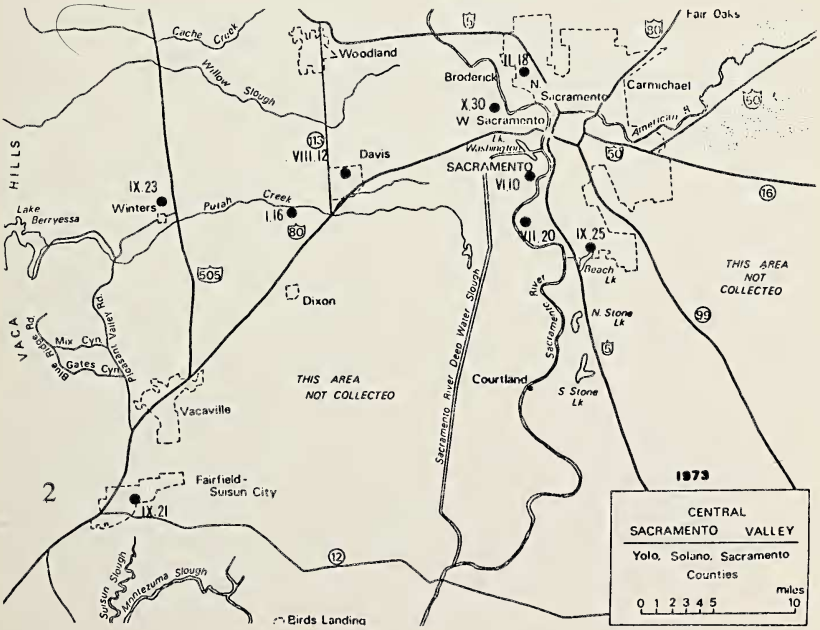

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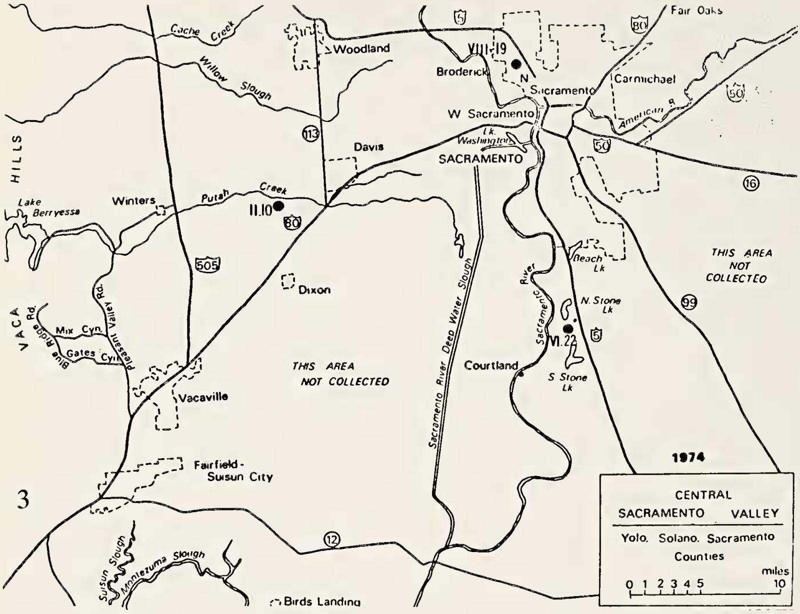
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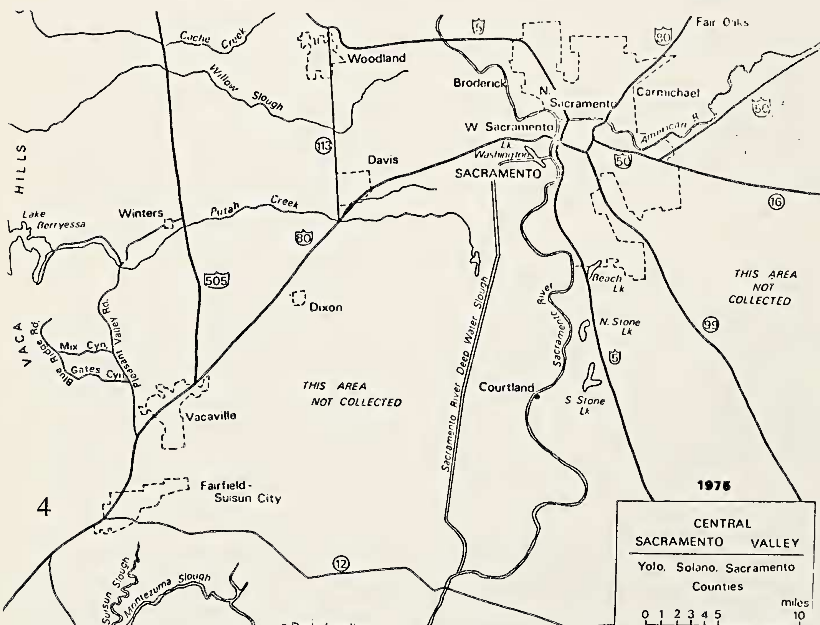
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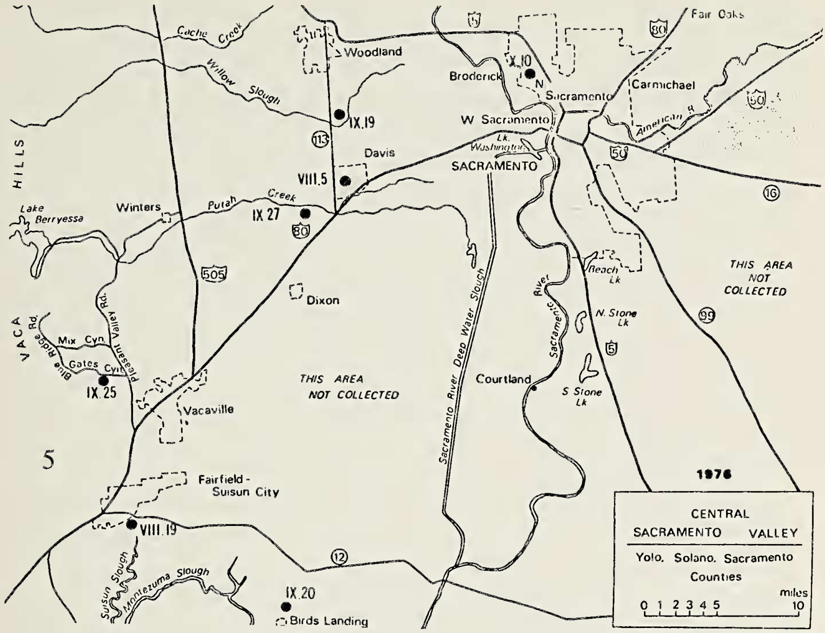
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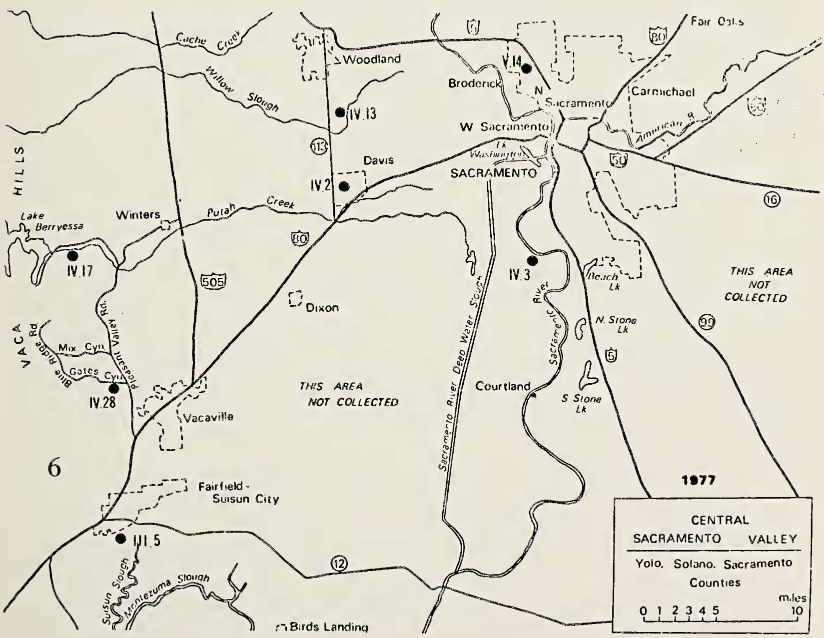
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ally high population levels, *P. protodice* never reached the Vaca Hills at the western edge of the study area, nor the Fairfield-Suisun area in 1972. However, incredible numbers flew in North Sacramento from late September to late October; in some fields they resembled a snowstorm. The flight there lasted to December 13. Although the first 1972 record at Putah Creek, near Davis, was not until 28 September, large numbers flew there during October and November (last record 22 December).

Autumn 1972 rains were early and excessive, with nearly 200 mm in October and November in locally severe thunderstorms. Severe cold in late November and early December was followed by more cold in late December, and continued heavy rains. Spring 1973 was generally cloudy, cool, and late, with cloudiness holding down daytime temperatures and preventing flight, and keeping night temperatures up, possibly favoring disease. Nonetheless, *P. protodice* overwintered successfully at North Sacramento, where the first brood was common from 18 February - 24 March, and at Putah Creek, 16 January - 15 March. Populations persisted at both places throughout 1973 without reaching 1972 levels. No other peripheral colonies founded in 1972 are known to have persisted into 1973. The overall pattern of late summer colonization resembled 1972, although the western edge of the Valley and the Suisun basin were reached. At the dredge tailings, autumn 1973 population levels were about half those of autumn 1972.

Winter 1973-74 was again very wet. Spring 1974 was mild and sunny; most spring butterflies emerged unusually early. Summer was cool, followed by a long, mild, dry autumn similar to 1971. This season was a disaster for the Checkered White. It was found at only three stations away from the dredge tailings, and populations were poor all season even there. One of the three stations was Putah Creek, where it overwintered so feebly (a second season) that no second generation appeared and the population became extinct; no matings may have taken place. There was no spring brood in North Sacramento, where it was not seen until mid-August.

Winter 1974-75 was wet at first, then turned warm and dry, and ended with a cold, cloudy, wet spring. Cool, moist weather persisted into summer 1975. *Pieris protodice* was apparently completely absent from the study area except on the tailings, where its numbers were even lower than the preceding year — up until autumn. The long, warm autumn of 1975 is generally

reckoned to mark the beginning of the California drought. In late September there were very substantial flights on the tailings for the first time since autumn 1973. These continued until mid December, although no outward dispersal was detected. After the mild and extremely dry winter, adults from overwintered pupae began emerging on the tailings on 25 January 1976, only five weeks after the last fall animal was seen. The early spring flight was very large for the season. Populations grew steadily on the tailings, with very high levels almost continuously through 19 November, and the last adult seen 26 December. Strays did not begin showing up off the tailings until August. Early records were at Davis (5 August) and Fairfield-Suisun (19 August), but none was seen at Putah Creek or in the Vaca Hills until the third week of September. The Suisun colonization resulted in a large fall brood, 6-16 October. Based on adult abundance and larval populations in autumn 1976, the pool of overwintering pupae was estimated to be slightly lower than in 1972-73 at the dredge tailings.

Winter 1976-77 was again mild and dry, notable for the number of clear days and the almost total absence of fog. No samples were taken in January or most of February, but on 27 February 1977, *P. protodice* was already abundant on the tailings (sex-ratio, condition, and presence of ova and larvae suggested it had been flying about two weeks). A few days later it was flying at Suisun City, having overwintered there for the first time in this study. By mid-May it was present essentially throughout the range it normally occupies in autumn of a favorable year, and breeding in most of this area. It did not overwinter in 1976-77 at either Putah Creek or North Sacramento, but first brood colonists must have reached Gates Canyon, Willow Slough, and Davis since numbers of fresh animals of both sexes were present there in April, an unprecedented observation. By early summer 1977 *Pieris protodice* was the commonest butterfly throughout the study area and had far surpassed its 1972-73 levels in most places. Snowstorm-like flights occurred near Winters, Woodland, and Dixon, reminiscent of the mass "migrations" of sulphur butterflies in alfalfa fields in the Imperial Valley in the 1940s and 1950s. Disturbed riparian habitats and roadsides supported large breeding populations. It was found abundantly at the head of the Valley at Turtle Bay, Redding, Shasta County, by 26 June; by 15 August it had spread to the 1500 m level in the Trinity Alps northwest of Redding.

At the same time as populations reached extraordinary highs away from the dredge tailings, numbers at the latter began to decline to abnormal lows. By 28 August *P. protodice* was as rare in Rancho Cordova as it had been in 1975. By the third week of August the impact of the two-year drought was conspicuously heavier on the east side of the Valley than elsewhere. Most of the coyote brush (*Baccharis,* Compositae) on the tailings was apparently dead, and both deciduous and live oaks were dropping leaves. The last yellow star thistles (*Centaurea solstitialis* L.) died, removing the principal nectar source. Such adults as could be found on the tailings were clustered around blooming plants of *Senecio Douglassii* DC. (Compositae) on the bank of the American River at Rossmoor Bar.

Following soaking rains between 15-20 September, numbers of butterflies rebounded on the tailings; many Cruciferous seedlings appeared, and some of the seemingly "dead" *Brassica* put on new growth; by 16 October densities were about one-fourth of what they had been on 17 October, 1976.

The Suisun City population also underwent severe strain. There are few *B. geniculata* at Suisun, and most of the large second brood reproduced on *Brassica nigra* (L.) Koch, a winter annual which was in flower at that time. By early summer it was gone, and populations of Whites collapsed in July. *Pieris protodice* managed to persist at a very low level through the second half of the season, and by 14 October numbers were increasing as hosts began to reappear.

HISTORY IN THE SIERRA NEVADA, 1972 - 1977

Phenological samples are also taken routinely along a transect paralleling Interstate 80, from Suisun City at sea level to over 2750 m on Castle Peak, north of Donner Pass. There are sampling stations at 1500 m and 2100 m on the west slope of the Sierra. In 1972 these were located at Marin-Sierra Camp and Boreal Ridge, respectively. In 1973 they were moved to Lang Crossing (South Yuba River) and Donner Pass, where they have remained ever since. *Pieris protodice* has been taken at all the stations along this transect at least as a rare stray, except in the alpine zone on Castle Peak. Comparisons can thus be made between population trends in the Sacramento Valley and in the adjacent

mountains. Rainfall and temperature on the west slope by and large vary in tandem with the Valley. This is not true on the east slope, which has a much more continental climate. Relevant weather station data are those for Blue Canyon at about 1500 m and the Central Sierra Snow Laboratory at 2100 m.

Sierran records of the Checkered White are given in Table 2. On the west slope it is rarely taken above the foothills. The mid-elevations are the wettest (Storer and Usinger 1971) and are also heavily forested, with few suitable open, disturbed habitats available. On the east slope *P. protodice* is an overwintering resident to at least 1700 m at the latitude of Highway 80. It is often common at Truckee, and survives the winter there despite very low temperatures. The Checkered White occurs much more commonly at Donner Pass than lower on the west side; this is presumably due to colonization from the east, where it is almost constantly present and has a shorter distance to disperse. Becker's White, *Pieris beckerii* Edwards, which is completely absent from northern and central California west of the Sierra, reaches Donner Pass and breeds some years (Shapiro, 1975b) and is unambiguously of east slope origin. Donner Pass is an "accumulator" of upslope dispersers from both sides (Shapiro, 1973, 1974b). It has not supported overwintering by *P. protodice* during this study.

A sibling species, *P. occidentalis* Reakirt, occurs from 1800 m upward on the west slope at the latitude of Interstate 80. It breeds in subalpine and alpine rocky and disturbed sites (Shapiro, 1976) but does not exclude *P. protodice* competitively below tree line (Shapiro, 1975b). In good years (including 1973, late 1976, and 1977) mixed flights occur at 2100 m. Donner Pass breeding by *P. protodice* may be influenced by Valley conditions, but it is difficult to account for 1975 colonizers when no other west slope records were obtained, and the pool of potential dispersers in the Valley was so low — unless they came from the east. Checkered Whites were at "normal" levels in Truckee and Reno in 1975.

When *P. protodice* occurs at 1500 m on the west slope, it is generally correlated with population levels in the Valley rather than at Donner Pass. On 17 April, 1977, two gravid females of the phenotype eclosing from overwintered pupae were taken ovipositing on *Lepidium* rosettes in a meadow at Lang Crossing.

There had been a large flight at Lang late the preceding summer, and these two animals are best explained not as colonizers but as overwintered individuals. A second brood flew in June, and the population persisted at moderate levels through late October. On April 22, 1977 a male of the *second* brood phenotype, presumably an upslope disperser from the east, was taken in Donner Pass. There was a large flight there, 1 July - 13 October.

Snow packs throughout the northern and central Sierra were at near-record lows in the winter of 1976-77. Warm spring weather began four weeks earlier than average at both 1500 and 2100 m. Normally flights cannot begin for a month after the onset of mild temperatures, because of the heavy snow pack; in 1977 actual flight conditions began in April even at Donner Pass. Normal temperatures and cloudiness in early spring would have prevented successful eclosion at Lang, where *P. protodice* does not normally overwinter.

DENSITY-RELATED FACTORS

Almost nothing is known of predation as a mortality factor on any stage of *P. protodice* in any population. In the Sacramento Valley insect parasitoids are rarely obtained from wild immatures before August. When population densities are very high, the rate of parasitization (by two Tachinids and one Braconid) has not exceeded 10%. The very rapid increases in White populations at Putah Creek in autumn 1972 or on the tailings in autumn 1975 suggest that its reproductive potential can far outstrip the parasitoids, making them important only at times of host scarcity — in a peripheral population, for example, the odds of successful overwintering diminish with every pupa subtracted from the pool by whatever factor.

Shapiro (1970) described density-related emigration from outbreak populations of *Pieris protodice*. When adults are very numerous in a restricted area, constant courting by males forces already-mated females down a gradient of male density, encouraging emigration. Under the extreme drought conditions of late summer 1977, both sexes emigrated from Rancho Cordova; this dispersal may have been density-independent. Many newly emerged Checkered Whites were seen in flower gardens in residential neighborhoods in Sacramento. Although females are often noted in such places during the autumn population peak,

it is extremely unusual to find males several kilometers from breeding habitat.

It is now possible to present a crude verbal model of the dynamics of *Pieris protodice* populations in the Sacramento Valley and Sierras.

At low elevations the persistence of a population depends on amount of overwinter survival. This in turn depends on (a) the size of the initial pool of pupae and (b) the winter weather. The pool of pupae is determined by (a) the demography of the population at the time of the last generation of the season and (b) mortality of the last brood of ova and larvae due to density-independent and density-dependent factors.

Large early spring populations, given favorable weather, give rise to rapidly growing late spring ones from which gravid females disperse under density-related pressure, founding new peripheral populations in areas where overwintering rarely occurs. This process may begin as early as the first flight (as in 1977), but is usually conspicuous by September and October.

The dredge tailings on the eastern edge of the Valley offer conditions for reliable overwintering, and thus serve as the ultimate source of colonists to other areas. Large peripheral populations in turn contribute colonists later in the season, founding still more peripheral populations, so that *P. protodice* occupies an increasing proportion of suitable habitats through the season until breeding is interrupted by the onset of winter. Density-independent emigration may occur from any population if host plants and/or nectar sources become unavailable; such emigration involves both sexes.

Colonizing females ascend the west slope of the Sierra Nevada as part of the generalized outflow in all directions from dense Valley populations. They may breed successfully at 1500 m and in very exceptional years, successful overwintering may occur. Colonizers reach Donner Pass (2100 m) more commonly from the east, not necessarily in phase with the dynamics of west slope and Valley populations.

DISCUSSION

How well does this picture correspond to the Ehrlich and

Birch mosaic model? Its general characteristics are very similar: a dynamic system of local populations coming and going stochastically, with a density-related (i.e. deterministic) input into colonization rate. However, extinctions are concentrated at the time of predictable winter stress; and the influence of density operates not through the number of habitats available for colonization — since saturation almost never happens — but the size of the "permanent" dredge tailings populations, which at least in the initial phases are the sole sources of colonizers. Except in 1977, overwintering was virtually confined to them.

The existence of these refuges is not unique to the Sacramento Valley. In the Philadelphia, Pa. - Camden, N.J. area on the Atlantic coast, near the northern boundary of that range, populations of *P. protodice* occur on waste ground, in railroad yards and waterfront areas near the Delaware River. Checkered Whites have bred here at least since the early 1930s, when Orazio Querci studied them; there are anecdotal reports carrying them back before the turn of the century. As in California, peripheral populations appear in vacant lots, along roadsides, and in old fields, extending even onto the Piedmont Plateau northwest of Philadelphia (Shapiro, 1966, 1970), but only one overwintered specimen is on record above the Fall Line although the spring brood occurs reliably near the river. The overall pattern of colonization and extinction is so similar that one suspects the presence of refuges may be a necessary condition for existence near the species border.

The Ehrlich and Birch model probably fits the dynamics of *P. protodice* with even less modification in the Basin-and-Range province and the southern Rockies. It is not known whether the Checkered White reached the Atlantic coast by itself or through human intervention (the type locality, "New York and Connecticut," is at its northeastern limit, where it is virtually confined to sandy beaches). Pacific Coast populations, however, are surely recent. At low elevations west of the Sierran crest there are no native summer Crucifers which could have sustained breeding; *P. protodice* is wholly dependent on weedy species which are thought to have entered California in the Mission Period (Frenkel, 1970). But in the Basin-and-Range province, where overall rainfall is lower, enough rain falls in summer thunderstorms to permit ephemeral blooms of annual (and some perennial) native hosts. In much of the province up-and-downslope colonizations may be essential for survival, but *P. protodice* can

Continued on Page 19